Phytopathology—1867-1942*

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The three decades 1850-1880 are noted for fundamental discoveries in the field of biology. In 1859 Charles Darwin published "The Origin of Species," a work which changed completely the viewpoint in biology. In 1865 Gregor Mendel published the results of his experiments on inheritance in peas, an account which made no impression upon his own generation, but proved to be the keystone of genetic investigation in the early twentieth century. Louis Pasteur, in 1855-1859, carried out his researches on fermentation, maintaining that the changes which occurred in various organic substances were the result of the activity of micro-organisms, instead of purely chemical processes in which the observed rods were supposed to originate as by-products. In 1860-1864 he was engaged in experiments on the problem of spontaneous generation. It was almost universally believed that the micro-organisms originated from the decomposition of higher plants and animals. The fungi associated with plant diseases were thought to arise from changes in the higher plants of unknown causal origin. In 1865-1870 he carried out his classic studies on the silkworm disease, demonstrating the microbic origin, not of one disease only, but of two. Robert Koch, in 1876, supplied decisive evidence that anthrax of cattle was due to a microscopic rod-shaped organism which had been associated with this malady by Devaine and Rayer in 1850. Koch's results were confirmed by Pasteur in 1881, who carried out his experiments on the prevention of anthrax of sheep by vaccination.

L. R. and C. Tulasne, in 1861, published the first volume of their standard work on the fungi, describing in great detail the life history and structure of the powdery mildews. In 1863 Anton de Bary worked out the life history of a powdery mildew, *Sphaerotheca castagnei,* on dandelion, describing the appearance of the sex organs. De Bary's most important work, however, was published in 1865, when he recorded heteroecism in *Puccinia graminis.* Previous to the work of Tulasne, de Bary, and others, the nature of the lower fungi was quite misunderstood and the idea that they were the cause of various diseases was not accepted. The demonstration of the polymorphism of the rusts, involving four or five spore stages, was a great advance in our knowledge. It was, of course, difficult for that generation to accept the view that a rust was not only parasitic, but required at least two different hosts in order to complete its life cycle of four or five types of spores.

* Presented at the 75th Anniversary Celebration of the Torrey Botanical Club at the Brooklyn Botanic Garden, Thursday, June 25, 1942.

Brooklyn Botanic Garden Contributions No. 99.

The idea that a plant disease might be due to the growth of one organism in another, resulting in the observed changes, was slow in developing. The more common view was that the growths observed followed rather than preceded the disease, which was assumed to be due to environal conditions—the weather, changes in temperature, moisture, and illumination, and other factors such as the time of planting the crop, the nature of the soil, and the application of fertilizers.

Perhaps the first disease of higher plants to be definitely connected with the growth of a fungous parasite was bunt of wheat. Tillet (1755) provided part of the evidence by showing that the "dust" from the bunted grains, when applied to the seed, in some way resulted in infected wheat heads. Prévost (1807) made a further advance by observing that the "dust" from the smut balls resembled fungous spores and germinated in a characteristic fashion. Kühn (1858) also studied the germination of the smut spores and observed the penetration of the germ tubes into the living wheat seedling. De Bary (1863), in his early experiments on the rusts, showed by inoculation of different spore forms that the disease followed in its characteristic symptoms. At the time of the outbreak of the potato blight in England and Ireland beginning in 1845, Berkeley was quite insistent that the fungus observed, now known as *Phytophthora infestans,* was actually the cause, although most of those with anything to do with the disease believed that environal conditions, particularly wet weather, were the primary factors.

Since 1867 there has been remarkable progress in working out the relation of fungi to diseases of plants. Further, other causes of disease have been demonstrated, since the bacteria are now known to produce many different types. We also have a whole group of diseases which are caused by a virus. So-called "physiologic" diseases, in no way associated with a living pathogen as a causal agent, are recognized. Many of these are due to the lack of some essential element such as boron, manganese, or some other.

It is interesting to note the parallel development in our knowledge of human and animal diseases along with the discoveries in the plant kingdom. Koch (1876) demonstrated that anthrax of cattle was due to a microscopic spore-producing organism and by 1881 Pasteur had developed his vaccines for the control of the disease. Klebs (1883) had observed the organism which causes diphtheria, Loeffler (1884) studied the organism and obtained pure cultures, Roux and Yersin (1888) discovered the toxin, and Behring and Kitasato (1890) isolated the antitoxin.

The organism causing bubonic plague or "Black Death" was seen independently by Yersin and Kitasato in 1894, and the accidental proof of its association with the disease came in 1898. About the same time, rats and fleas were found to be the carriers. The organism which causes tetanus was observed by

Nicolaier (1884), Kitasato (1889) giving the proof of its causal connection. One of the most striking developments was in connection with malaria, known in various forms since ancient times. Laveran (1880) had come to the conclusion that its spread was associated in some manner with mosquitoes and Ross (1898) demonstrated conclusively that a species of *Anopheles* was the carrier and, further, that the causal organism underwent cyclic changes in both mosquitoes and man. Soon after, the method of distribution of yellow fever was discovered. Finlay (1881) believed that mosquitoes might be the carrier and Reed and his associates (1900) demonstrated that the mosquito *Aedes calopus* was the responsible agent. The application of these discoveries led to the elimination of yellow fever as a serious disease in most parts of the world.

The story of plant pathology contains many chapters which are concerned with disastrous diseases of economic plants. Frequently the outbreaks are due to the introduction of susceptible hosts to new regions where an indigenous parasite attacks them. In some cases a pathogen is carried to other parts of the world, where it finds susceptible hosts.

The potato blight, which appeared in England and Ireland in 1845, focused attention on this particular disease and led to great advances in plant pathology, although the immediate results were disastrous for the people who depended on potatoes for their food. Frequently since then potato blight has occurred in destructive forms, and continues to be under constant investigation for methods of control. The coffee disease, caused by *Hemileia vastatrix,* appeared in Ceylon about 1869 and during the following years proved to be very destructive. The final result was that the growing of coffee was given up in Ceylon, being replaced by tea plantations, and coffee culture developed in Brazil.

The American chestnut blight was first observed in Greater New York in 1904 and the evidence is that the causal organism, *Endothia parasitica,* came from the Orient on nursery stock. Since the first appearance of the disease our native chestnut tree has been practically wiped out. The white pine blister rust caused by *Cronartium ribicola* was first noted in America in 1906 on three year old white pine seedlings imported from Germany. Previous to that, the disease had spread widely through Europe on the American white pine, which had been introduced. Shortly after the pathogen appeared in America it spread far and wide on the five-needle pines and necessitated radical methods of control, which involved the attempted eradication of wild and cultivated species of *Ribes* adjacent to the white pine forests.

The rust of wheat caused by *Puccinia graminis* doubtless accompanied the introduction of wheat into new regions and, wherever wheat is grown, damage has been done. In the United States, 1904, 1916 and 1935 are especially noted for the destructive outbreaks.

Since 1867 progress in plant pathology has proceeded along several lines.

1. Life history and classification of the fungous pathogens. Following the demonstration of heteroecism in the stem rust of wheat by de Bary (1865), the life histories of many rusts were determined. De Bary (1866) demonstrated heteroecism in the crown rust of oats caused by *Puccinia coronata*, the aecial stage occurring on species of *Rhamnus*. Oersted (1865) established the hereroecism of *Gymnosporangium sabinae*. Almost every year one or more connections were established, largely by workers in Europe. Halsted (1886) and Thaxter (1887) showed that the life cycle of *Gymnosporangium juniperi-virginianae* required the red cedar and the apple for its completion. Klebahn (1888) demonstrated the connection between the white pine and species of *Ribes* in the blister rust, *Cronartium ribicola*, and for a period of years he devoted himself to a study of heteroecious types, by 1904 listing 178 species belonging to 11 rust genera. Dietel (1918) listed a total of 264 heteroecious rusts. Arthur (1900-1921) was an active worker in growing cultures of various rusts on different hosts in order to determine their life history, and demonstrated that approximately 50 different North American rusts were heteroecious, in 1934 listing 153 species belonging to 14 genera in his Manual of the Rust Flora of the United States and Canada.

Along other lines, great advances in our knowledge of the rusts have been made. Eriksson (1894) discovered racial specialization. Blackman (1904) and Christman (1905) described what they interpreted as a method of sexual reproduction at the base of the young aecial cups. It remained for Craigie (1927-1933), in a series of papers, to demonstrate the relation of the pycnia and the young aecia in the life cycle, thus completing the main outlines of the life history of this pathogen. There was an immediate application of these studies in connection with the possible origination of new races of rusts.

The main facts in the life history of the bunt of wheat were established by Tillet (1755), Prévost (1807) and Kühn (1858). A further point in the method of distribution was brought out by Woolman and Humphrey (1924) in which they showed that soil contamination was an important factor in our Northwestern States.

The life history of the other smuts of cereals has also been worked out. L. R. and C. Tulasne (1847) differentiated some of the main types. Jensen (1888) devised the hot water treatment for the oat and barley smuts and distinguished two species on the latter host and Kellerman and Swingle (1890) separated the covered smut of oats from the loose smut. Brefeld (1870-1912) published 15 volumes recording the results of his labors on the smuts and other fungi. Of special significance was the demonstration of the flower infection method in the loose smut of barley and wheat by Brefeld and Falck (1905). Zade (1924) added to our knowledge of the method of distribution of the loose smut of oats, suggesting that to a large extent the wind-blown spores germinated in the flowers, finally forming a resting stage, so-called "gemmae," beneath the glumes, which later produced the infection in the young seedling.

Leveille (1851) brought out his standard work on the powdery mildews, describing the genera which, for the most part, are accepted today. De Bary (1863) worked out the main points in the life history, describing the sexual organs and Harper (1895, 1896, 1905) investigated the cytology of sexual reproduction and ascospore formation. From the taxonomic standpoint, Salmon's monograph, published as a Memoir of the Torrey Botanical Club in 1900, was a landmark in our knowledge of the powdery mildews.

Among the downy mildews, potato blight has been the subject of intensive investigation wherever potatoes are grown. Studies have been concerned not only with the pathology and the control of the organism, but also with its life history. Berkeley, in the late 1840's, made the first detailed studies. It remained for Clinton (1911) to discover the oospores, Jones, Giddings, and Lutman (1912), and Pethybridge and Murphy (1913) adding further data on the conditions necessary for sexual reproduction. Gaümann (1923) brought together the results of his detailed studies on the genus *Peronospora*.

Great strides have been made in the large group of the Ascomycetes and the connection between the conidial and ascospore stages of many have been established. L. R. and C. Tulasne (1853) described in detail the life history of *Claviceps purpurea*, which causes the ergot of rye. Aderhold (1894) and Clinton (1901) established the connection between the common apple scab organism and the ascocarp known as *Venturia inaequalis*. Norton (1902) discovered the apothecia of the brown rot of stone fruits, although Schroeter (1893) concluded that the species of fungi causing brown rot belonged in the genus *Sclerotinia* and Woronin (1898) showed that there were two distinct species of this genus, *S. fructigena* and *S. cinerea*.

2. Physiologic specialization. Proper identification of hosts is basic to an advance in the knowledge of pathogens which cause disease. Taxonomists have been concerned largely with genera and species, while the agronomists and horticulturists have been interested in the cultivated varieties. Students of the parasitic fungi must necessarily be familiar with the host plants upon which they grow since, in works dealing with their classification, the keys are largely based upon the proper host identification, and Arthur's recent Manual of Rusts (1934) is a fine illustration.

One of the great advances in pathology since 1867 is the demonstration of physiologic specialization. Schroeter (1879) called attention to this phenomenon in connection with certain rusts on *Carex*. The first important work, however, was that of Eriksson (1894) who made an intensive study of *Puccinia graminis* from the cultural standpoint. On the basis of his experiments, he recognized 6 *formae speciales—Avenae, Secalis, Tritici, Airae, Agrostidis,* and

Poae. Another step was taken in 1917, when Stakman and Piemeisel found that *P. graminis tritici* consisted of at least more than one specialized race or physiologic form. By 1922, 37 specialized races of this pathogen were known and by 1934 not less than 127 had been isolated, and now the number is about 160. Similar specialization has been found in other groups of grass rusts. In crown rust of oats Murphy (1933) listed 33 races and Johnston et al (1942) brought together the data for *Puccinia rubigo-vera tritici*, recording 129 races known in various parts of the world. Most rusts which occur on several species of grasses, particularly if they belong to different genera, show the phenomenon of specialization. It is interesting, however, that *Puccinia subnitens* does not, the spores from the uredial and telial host being able to infect aecial hosts belonging to 15 genera, distributed among 6 different families.

Specialized races of the powdery mildews were first recorded by Marchal (1902) when seven were differentiated on the basis of cultural experiments—*Avenae, Agropyrae, Bromi, Hordei, Poae, Secalis,* and *Tritici,* all being limited to one or more species of a single genus. Salmon (1903) and Reed (1906-1916) extended the evidence for specialization within this mildew. A further step was taken by Mains and Dietz (1930) when they showed that *Erysiphe graminis hordei* consisted of at least 5 distinct races, and Mains (1933) found 2 races of *E. graminis tritici.*

The first evidence of specialization in the smuts was recorded by Zillig (1921) in *Ustilago violacea*. Faris (1924) demonstrated the occurrence of 5 physiologic races in the covered smut of barley, *U. hordei,* and Reed (1924) demonstrated races in both loose and covered smuts of oats. At the present time 30 specialized races of loose smut and 14 of covered smut are known. Faris (1924) demonstrated specialization in the bunt of wheat, his data being extended by Reed (1927, 1928) when 5 races of *Tilletia levis* and 6 of T. *tritici* were differentiated. Rodenhiser and Holton (1937) listed 8 physiologic races of *T. levis* and 11 of *T. tritici.* Such specialization has also been found in *Sphacelotheca sorghi, Sorosporium reilianum, Ustilago tritici,* and *U. zeae.*

Physiologic specialization is an essentially universal phenomenon among the pathogenic fungi. In any case where a morphological species of a fungus occurs on several hosts, it is almost certain that strains or races exist which are limited in their capacity for producing infection.

Ward (1903), in his study of the brome rust, *Puccinia dispersa,* raised the question whether "bridging hosts" existed, publishing data which he regarded as evidence that a particular race of brome rust might be grown on a specific host and then be capable of infecting other brome grasses which originally it was not able to do. Salmon (1904) published similar data for the powdery mildew on the brome grasses. For many years no clear-cut confirmation of these conclusions was available. The general idea, however, was held in connection with the rusts that the aecial host might be a meeting place for different races, resulting in a changed capacity for infection in the uredial stage. It is now known that on the aecial host hybridization of the races of the pathogen may take place, and thus new races arising might differ greatly in their capacity for infection.

Reddick and Mills (1938), in connection with the potato blight organism, have suggested that when it is grown on partially resistant hosts, it may acquire an ability to infect a wider range of varieties, thus bringing to the fore again the question of bridging hosts.

3. Environal factors. Before 1867 the view was that environal factors were the principal cause of plant diseases and, as a corollary of this, the fruiting bodies of the fungi which appeared upon the plant followed the disease. Epiphytotics, such as the potato blight in the 1840's were largely attributed to the weather.

We now recognize the very great importance of environal factors as predisposing the appearance of a diseased condition; in fact, three different things are necessary: (1) a susceptible host, (2) a causal agent such as a fungus, bacterium, or virus, and (3) environal factors that are favorable for the establishment of the relation between the two. We must emphasize the interrelations of environal factors, including soil temperature, moisture, and reaction, since it is impossible to find a fixed optimum for any one, regardless of the possible associated variables.

While we know that the real cause of many diseases is due to specific organisms, we also know that particularly disastrous epiphytotics occur only under peculiar environal relations. Jones, Giddings, and Lutman (1912) worked out the relation of weather conditions to the development of potato blight. The prevalence of wheat bunt depends upon low soil temperature at the time of seeding. Oat smuts are not as destructive, ordinarily, in the Eastern United States as in the Western.

Intensive studies on the relation of environal factors to plant diseases have been made. The relation of temperature and moisture to the infection of wheat by the two species of *Tilletia* was made by Hecke (1909), Heuser (1922), Munerati (1922), Hungerford (1922), and Faris (1924). Faris (1924) studied the temperature and moisture relations for infection of barley by the covered smut, Bartholomew and Seymour (1923) for the loose smut of oats, and Reed and Faris (1924) for the covered smut of oats and the loose and covered smuts of sorghum.

On the establishment of the Department of Plant Pathology at the University of Wisconsin, Professor L. R. Jones and his students conducted extensive studies over a period of years, with elaborate equipment, on the influence of environal factors on the development of many plant diseases. While emphasis was laid on temperature, other factors such as moisture and soil conditions were determined in the case of cabbage yellows, flax wilt, tomato wilt, tobacco root rot, stem canker of potato, and other diseases. An interesting result was observed in seedling blight of cereals caused by *Giberella saubinetii*, an organism causing the disease in both corn and wheat. In corn, severe infection occurs at 16° C. and only slight infection at 24°, while in wheat the temperature relations are reversed. Jones, Johnson, and Dickson (1926) have summarized the investigations.

Seasonal development influences the reaction of many plants to a particular disease. Waterhouse (1929) found that barley hybrids gave different results in winter and summer months, when inoculated with *Puccinia anomala*. Some families in winter gave a normal ratio of 3 resistant to 1 susceptible, while in summer the progenies failed to show the expected segregation. Harrington (1931) found that a series of progenies of a cross of Marquillo × Marquis showed susceptibility as dominant with a race of *P. graminis tritici* at a high temperature, while at a low temperature resistance was dominant. Mains (1934) found that hybrids between Michigan Amber and Chinese wheat were difficult to classify in their reaction to a race of *Erysiphe graminis tritici* when grown in the spring, while it was easy to group the hybrid lines when grown in the winter. One parent, Michigan Amber, was resistant in the winter and more or less susceptible in the spring. Gordon (1930, 1933) found that some oat varieties showed no significant differences in their reaction to certain physiologic races of *Puccinia graminis avenae* when grown at four different temperatures from 57.4° to 75.4° F. The Joanette variety, however, was very resistant to some other races at low temperatures and susceptible at high. Peturson (1930) found that Red Rustproof oats was resistant to a race of *P. coronata avenae* at 57° and susceptible at 70 and 77°. Four other varieties were fully susceptible at all three temperatures, while a fifth variety was resistant. Another aspect of the problem was brought out by the work of Goulden, Newton and Brown (1930). Some wheat varieties showed no essential differences in reaction to particular physiologic races of *P. graminis tritici* in the seedling and in the mature plant stage. Other varieties, however, differed markedly in resistance in the two stages of plant growth. These results have been confirmed by other investigators.

4. Diseases caused by bacteria and other organisms. In addition to the diseases of plants caused by fungi, it is now known that many important diseases of plants are caused by bacteria and other organisms.

Let us recall the fact that Koch (1876) demonstrated conclusively that anthrax of cattle was caused by bacteria. In the period 1878-1883 Burrill carried out his studies which showed the relation of fire blight of pears to particular bacteria. Then followed in rapid succession other demonstrations of the relation of bacteria to plant diseases—Wakker (1883-1889), yellow disease of hyacinths; Smith (1897) and Russell and Harding (1898) black rot of cabbage; Stewart (1897) bacterial wilt of sweet corn; Smith and Townsend (1907) and later publications by Smith and others on crown gall. These, and such other diseases as blight of beans, citrus canker, soft rot, cucurbit wilt, black leg or black rot of potato, red-stripe disease of sugar cane, and wildfire of tobacco, have all been associated with bacteria. Smith (1905, 1911, 1914) published three large volumes dealing extensively with the bacterial diseases and in 1920 published his summary. Elliott (1930) listed 177 species of bacterial plant pathogens—13 caused by *Aplanobacter,* 53 by *Bacillus,* and 111 by *Bacterium.*

It is also interesting to recall the controversy between Dr. Alfred Fischer and Dr. Erwin F. Smith in 1899. The former maintained that bacteria did not cause disease in plants, while Smith affirmed their causal connection.

Other organisms have also been associated with plant disease. Club root of cabbage, caused by *Plasmodiophora brassicae,* has been studied by Woronin (1878), Lutman (1913), Kunkel (1918), and others. Root knot or root gall, caused by nematodes, was first observed by Berkeley (1855). Greef (1872) described the nematodes, Frank (1885) and Atkinson (1889) gave further details on the disease and the causal organism. The nematode disease of wheat was found by Johnson (1909) in California and by Fromme (1917) in Virginia. Byers (1918-1920) has made detailed studies.

5. Virus diseases. A separate chapter in plant pathology deals with the virus diseases of plants. The first scientific studies were concerned with the tobacco mosaic, which has continued to be a favorable subject of many investigators. Mayer (1886) discovered the infectious nature of the juice of mosaic tobacco plants, Ivanowski (1892) discovered that the infectious principle could pass through a Chamberland filter, which held back bacteria, and Beiyerinck (1898) extended the work, introducing the term "contagium vivum fluidum." Many plant diseases are caused by a filterable virus, among them aster yellows, curly top of beet, sugar cane Fiji disease, peach yellows, stunt disease of rice, mosaics of sugar cane, cucumber, hop, lily, and potato. We may note in passing that Loeffler and Frosch (1898) established the first causal connection of a virus to a disease of animals, the foot and mouth disease of cattle.

Studies have been made on the methods of transmission of the filterable viruses, being distributed by grafting, budding, and on the seed, as in the case of the legume mosaic. A most interesting development is the discovery of insect vectors. Takami (1901) found that the stunt disease of rice which was often destructive in Japan, sometimes resulting in crop failures involving famines, was caused by the feeding of the leaf hopper, although the actual virus was not discovered until 1908-1909. Aphids and leaf hoppers are very common vectors. Usually, there is a high degree of specialization in the carrier, a specific insect being responsible for a particular disease. Remarkable progress has been made in the study of the nature of the viruses. Duggar, Kunkel, Smith, Stanley, and many others have made important contributions.

6. Disease resistance. From the earliest times it was observed that species and varieties varied in their susceptibility to disease, and the resistant ones were selected in order to minimize loss. In recent years great progress in the selection of these has been made and programs have been developed in the field of plant breeding for combining the resistant quality with other desirable characters. Success is dependent upon the close cooperation of the plant breeder and the pathologist.

Orton (1899 and later) stressed the value of types of watermelons resistant to the wilt disease and by 1913 had developed commercial varieties. Norton (1910) obtained varieties of asparagus resistant to the rust. Jones and Gilman (1915) began their work on cabbage resistant to yellows. Edgerton (1918) and Pritchard (1922) have developed wilt-resistant tomatoes. Jagger and Scott (1937) obtained cantaloupe varieties resistant to the powdery mildew.

Finding resistant stock is the first step in any breeding work. The species or varieties may be brought in from other countries and used in the program. Wild potatoes have been sought in Mexico and Peru, and melons from India have proved useful. Graves is finding chestnuts from the Orient useful in developing hybrids of our native chestnut which are resistant to blight. Barley, oat, and wheat varieties have been carried from one part of the world to another and serve as basic stock in breeding programs.

In most groups of economic plants, studies on varietal resistance have been made, for example: Reed, Griffiths and Briggs (1925) on the resistance of oat varieties to both loose and covered smuts, Reed and Melchers (1925) on the resistance of sorghum varieties to the covered smut, and Tisdale et al. (1923) on the resistance of varieties of wheat to the flag smut, and (in 1925) to bunt. At the Institut für Pflanzenbau und Pflanzenzüchtung, Halle-Saale, students of Director Th. Roemer have made similar studies of several of the cereal smuts.

Rieman (1939) stated that about 80 resistant varieties of vegetable crops had been developed and at least 20 of these were recognized by the trade, including asparagus resistant to rust, snap beans to mosaic, cabbage to yellows, corn to Stewart's bacterial disease, lettuce to brown blight and powdery mildew, peas and tomatoes to fusarium wilt. Coons (1937) estimated that about one-quarter of the acreage devoted to 17 important crops in the United States was planted to disease-resistant varieties.

Breeding for disease resistance is a difficult and time-consuming procedure and there are many hazards by the way. Frequently new physiologic races of the pathogen appear. This is well illustrated in potato breeding for blight resistance. The first attempts to obtain resistant varieties were made in the late

1840's and ever since efforts have been continued to secure resistant varieties. In a few cases promising results were secured, especially when a new breeding stock was obtained from Mexico or Peru. Since 1918, Reddick in the United States, Salaman in England, Müller and Schick in Germany, and workers in Russia, have developed blight-resistant potato breeding programs. However, the discovery of specialized races of the pathogen in 1933 by Müller and by Miss O'Conner and Peterson (1933) have made the program more difficult. Another example of the difficulties in the successful development of resistant varieties is found in breeding oats for smut resistance. The variety Victoria was imported from Uruguay by the United States Department of Agriculture in 1927. After its introduction it proved to be resistant to all races of loose and covered smut known at that time. It was crossed with other varieties and by 1940 many valuable selections had been obtained which combined smut resistance with other desirable qualities. The discovery of a new race of smut in 1941, which attacks Victoria and most of the selections derived from its crosses, necessitates a new breeding program.

The genetics of disease resistance has been investigated by many workers. Biffen (1904) early published data on the yellow rust of wheat, *Puccinia glumarum,* which indicated that the inheritance of resistance followed the Mendelian laws. The rusts have been suitable for such studies, since the results from an experiment may be secured in seven to ten days. However, environal factors must be carefully considered. Many hybrids have been studied by Hayes et al. (1920), Harrington and Aamodt (1923), Clark and Ausemus (1928), Goulden et al. (1928), McFadden (1930), as well as other investigators. Sometimes the results have indicated a simple relation, while in others the genetic situation is quite complex.

The smuts of cereals have been favorable subjects for the study of the inheritance of disease resistance. One of the difficulties, however, is the long period of time required for securing the data, and another is the great importance of the control of environal factors at the time of infection. Gaines (1923) obtained a complicated situation in his studies of the genetics of bunt resistance. Briggs (1926 and after) secured quite clear-cut results which usually indicated monohybrid ratios. He reported, however, the occurence of several factors for resistance found in different varieties. Crosses between resistant and susceptible varieties of oats have been studied with reference to their resistance to loose and covered smuts, beginning with Wakabayashi (1921), Gaines (1925), and Reed (1925). Many different hybrids have been studied by workers, and the results sometimes indicate clearly a single factor difference, while in other crosses two, three, or even more factors are required to explain the data. Mains (1934) studied the resistance to powdery mildew of wheat hybrids and Briggs (1935 and later) carried out a series of experiments with different hybrids of barley, sometimes obtaining simple relations, but identifying several distinct factors for resistance to a specific race of the powdery mildew.

7. Disease control. Viewed by the practical man, the control of disease is the primary consideration, and the emphasis is placed on securing adequate methods for avoiding the losses due to the destructive diseases. The selection of resistant varieties is one method of procedure, but many others have been employed. The prevention of disease, rather than an attempted cure of infected plants, is recognized as of first importance. Ward (1882), in connection with the coffee disease, clearly emphasized the idea of preventive treatment. It is essential that the toxic material be applied so that it is on the leaves when the spores of the pathogen are germinating. Whatever material is used, it must be applied at the right time.

In a few cases curative measures are successful. In loose smut of wheat and barley, the invasion of the parasite occurs just after the period of pollinization and as the grain ripens the fungus passes into a dormant condition, and may be killed by the hot water treatment. There are a few other illustrations, particularly in the case of virus diseases, as discovered by Kunkel.

Previous to 1867 there were two diseases of plants which were more or less effectively controlled by chemical substances. One was the powdery mildew of the grape by the use of sulphur, discovered by Tucker (1847), and the other the bunt of wheat by a method of seed treatment with salts of copper, as worked out by Prevost, Kühn, and others. Since 1867 great strides have been made in the control of diseases by chemical means. Many sprays and dusts have been utilized, one of the most important being Bordeaux mixture, discovered by Millardet in 1882, which was effective against the downy mildew of the grape. This spray, with modifications, is still one of the standard materials in the control of many diseases. Lime-sulphur was accidentally discovered in 1885 as an effective control of the peach leaf curl, Pierce (1900) giving the history of its use. Scott (1908) reported experiments on the value of self-boiled lime-sulphur, which was effective in the control of peach scab and brown rot, and was successfully used to control apple scab in 1910. Great emphasis has been placed upon the use of dusts instead of sprays in the control of fruit diseases. Whetzel and his associates have been active in the development of suitable dusts.

Copper, mercury, and sulphur remain, at the present time, the principal materials for the chemical control of disease. However, great advances have been made in the use of these elements in new types of compounds and in the physical make-up of the dust or the spray. Investigations have been carried out on the proper methods of applying the material, the discovery of suitable spreaders and stickers, and methods of control involving the combination of insecticides and fungicides. Important changes have occurred in developing suitable spraying and dusting machinery, and elaborate schedules for applications for the control of various diseases and insect pests have been worked out.

Great advance has been made along the line of seed treatments. Formaldehyde was first successfully used by Bolley (1897) for the control of oat smut, and Haskell (1917) devised the spray method, thus solving the problem of the wet grain. Copper carbonate dust was introduced for the control of bunt of wheat by Darnell and Smith (1915) in Australia and Mackie and Briggs used this material successfully in the United States in 1920. Riehm (1913) discovered the value of organic mercury compounds, as chlorphenol mercury, in the control of smut diseases. Important advances in the use of the organic mercurials have been made, utilizing such substances as uspulun, germisan, chlorophal, and semesan.

The application of heat has proved successful in the case of some diseases. Jensen (1882) partially controlled the potato blight by heating the tubers. In 1888 he applied the hot water method to the seed of oats and barley for the prevention of smut. The hot water method was improved by Appel and Riehm (1911) and by the pathologists in the United States Department of Agriculture since 1920. Kunkel (1936) found that heat treatment is effective in the control of peach yellows, diseased plants recovering after being held for some time at 35° C. The yellows of periwinkle disappeared if infected plants were held 38°-42° C. for two weeks (1941).

8. Research and teaching. With rare exceptions, previous to 1867 botany was not recognized as an important subject for research or instruction in colleges and universities. Little attention was paid to pathology, most of the work being done in Europe. Since 1867, however, research and teaching have greatly expanded, not only in Europe but also in the United States. Thomas Taylor was appointed microscopist in 1871 in the Department of Agriculture and in his first report published an illustrated article on the diseases of grape, pear, and peach trees and lilacs. In 1886 a Section of Vegetable Pathology with Frank Lamson-Scribner as Chief was organized in the Division of Botany, and the first bulletin was on the fungous diseases of the grape vine. E. F. Smith, an assistant in the Division, started his investigations on peach yellows, the first bulletin on this disease appearing in 1891. Farlow (1874) began his investigations and teachings along pathological lines. Burrill (1878) began his studies on pear blight.

In 1888 B. T. Galloway was appointed Chief of the Division of Vegetable Physiology and Pathology, heading the Bureau of Plant Industry when it was established in 1901. Further reorganization of the botanical and pathological work of the Department has taken place, but diseases of plants continue to occupy the time of many investigators. The importance of pathology is emphasized by the organization of the Division of Cereal Crops and Diseases, Division of Fruit and Vegetable Crops and Diseases, and the other Divisions of the Bureau of Plant Industry.

The Rockefeller Institute for Medical Research in 1932 established at Princeton, New Jersey, a laboratory for research in plant pathology, an institution largely devoting its attention to the virus diseases of plants.

In the State Universities, Agricultural Colleges, and Experiment Stations, the study of plant diseases has been given increased attention. Before 1900, the botanists of the institutions may have carried on investigations on some diseases of plants. Later, men were appointed to devote their entire time to pathology. No State, however, had a pathologist until after 1900, although fine pathological work was done by Burrill, Arthur, Jones, and others. The first separate Department of Pathology was organized at Cornell in 1907 under Professor H. H. Whetzel. In 1909 Professor L. R. Jones headed the Department of Plant Pathology at the University of Wisconsin. In California Dr. R. E. Smith in 1903 was appointed Assistant Professor of Plant Pathology in the Department of Botany, and in 1907 Dr. E. M. Freeman received the title of Assistant Professor of Botany and Pathology at the University of Minnesota. Pathology, in most institutions, is a part of the Department of Botany, although in a few it is separated.

There has been a great increase in the facilities for the encouragement and publication of research. The American Phytopathological Society was founded in 1908 with about 200 charter members, the enrollment in 1941 consisting of 1120 members.

Most botanical journals publish papers on plant pathology. A few, however, are devoted largely to this phase of botany: Zeitschrift für Pflanzenkrankheiten (1891) edited by Dr. Paul Sorauer; Phytopathology (1911) first edited by L. R. Jones; Société de Pathologie Végétale de France (1914); Review of Applied Mycology (1922) edited by E. J. Butler; Phytopathologische Zeitschrift (1929) edited by E. Schäffnit.

The Bureau of Plant Industry, United States Department of Agriculture, from 1901-1913 published 285 Bulletins, as well as Circulars, many of which were devoted to pathological subjects. The Journal of Agricultural Research succeeded the Bulletins in 1913, and has published many papers along pathological lines. In addition, the Department still continues to issue Technical Bulletins in pathology, as well as in related botanical and agricultural fields. The Agricultural Colleges and Experiment Stations have issued many Circulars, Bulletins, and Memoirs, on plant diseases.

Previous to 1867 there were very few textbooks dealing with pathology. Among the earlier were those of Unger (1833); Weigmann (1839); Meyen (1841); Berkeley (1854-1857); and Kühn (1858). Sorauer published the first edition of his Handbuch der Pflanzenkrankheiten in 1874, consisting of a single volume. In 1933 the first volume of the sixth edition of the greatly expanded work appeared. Hartig (1882) published his text on tree diseases. Kirchner (1890), von Tubeuf (1895), and Frank (1896) wrote general texts. Since 1900 many texts have been published, among the first being Duggar's Fungous Diseases of Plants (1909). Some of the texts cover the general field, while others are limited, dealing either with diseases of fruit trees, vegetables, cereals, ornamental plants, or trees.

One of the most important developments in the advancement of plant pathology and the control of plant diseases was the passage of legislation. Great Britain (1877) passed its Destructive Insects and Pests Act against the Colorado potato beetle and, in 1907, against all insect pests, the first ruling being applied against American gooseberry mildew and the wart disease of potato. The United States Department of Agriculture (1912) established a Federal Horticultural Board and issued the Quarantine Act. The first orders were against white pine blister rust and the wart disease of potato.

Brooklyn Botanic Garden
Brooklyn, New York

At the meeting at the Brooklyn Botanic Garden on Thursday, June 25, a fourth paper was presented by Dr. A. F. Blakeslee on "Technical Applications of Genetics in Plant Breeding in 75 Years." Unfortunately this paper is not available for publication.